# KIRTLANDIA®

# ISOLATED TETRAPOD REMAINS FROM THE CARBONIFEROUS OF WEST VIRGINIA

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## Abstract

In addition to *Greererpeton* (Amphibia; Temnospondyli) and *Protero-gyrinus* (Amphibia; Anthracosauria), Carboniferous tetrapod fossils from Greer, West Virginia, include fragmentary remains attributed to *Crassigyrinus, Eoherpeton,* and at least one other taxon, a large temnospondyl amphibian.

The description of additional tetrapods from Greer demonstrates that in terms of its taxonomic diversity it resembles other Euramerican Carboniferous localities which span the Viséan-Namurian boundary.

## Abstract

In addition to *Greererpeton* (Amphibia; Temnospondyli) and *Proterogyrinus* (Amphibia; Anthracosauria), Carboniferous tetrapod fossils from Greer, West Virginia, include fragmentary remains attributed to *Crassigyrinus*, *Eoherpeton*, and at least one other taxon, a large temnospondyl amphibian.

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## Introduction

The first vertebrate remains recovered from Carboniferous deposits within a limestone quarry operated by the Greer Limestone Company near Greer, West Virginia, were discovered in 1948 by an amateur, L. R. Collins, (Hotton 1970). The quarry lies just north of State Route 7, about 10.5 km southeast of Morgantown, Monongalia County (Universal Transverse Mercator Grid, Zone 17 NJ 991809). More detailed descriptions of the locality are provided by Hotton (1970) and Romer (1969, 1970). In July of 1968, J. J. Burke and W. E. Moran discovered, in a slab which had fallen from the quarry wall, the incomplete remains of a new temnospondyl amphibian, *Greererpeton burkemorani* Romer, 1969. By 1969, this quarry was recognized as yielding some of the oldest non-ichthyostegalian tetrapods. In 1970, A. S. Romer and N. Hotton III published descriptions of the new anthracosaurian amphibians from Greer, *Proterogyrinus scheelei* and *Mauchchunkia bassa* respectively. Because no consistently unique features distinguish the latter from the former, Holmes (1984) concluded that *Machchunkia* was the junior synonym of *Proterogyrinus*.

Between 1969 and 1973, field parties from the Cleveland Museum of Natural History under the direction of D. H. Dunkle recovered a large number of vertebrate skeletons from a restricted bed within the quarry (Fig. 1). The main bone-bearing layer, exposed for some 15m along the vertical face of the quarry, contained a nearly solid mass of fish and amphibian remains. *Greererpeton*, represented by at least 60 individuals, was by far the most common vertebrate recovered. Several virtually complete specimens were preserved literally head-to-tail (Godfrey 1986). This deposit also produced articulated skeletons of the lungfish *Tranodis castrensis* Thomson and articulated skeletons of the anthracosaur *Proterogyrinus scheelei* Romer.

In addition to these spectacular finds, the Cleveland Museum of Natural History (CMNH) and the Museum of Comparative Zoology (MCZ) recovered numerous spines of the acanthodian *Gyracanthus*, one shark spine (M. E. Williams, CMNH, personal communication), disarticulated remains of palaeoniscoid fishes, isolated elements of a large rhizodont crossopterygian, cf. *Strepsodus,* and isolated postcranial remains of several heretofore undescribed tetrapods. This paper deals with only the undescribed tetrapod remains.

Vertebrate remains at Greer were recovered from the Bickett Shale (Bluefield Formation), which forms the lower subdivision of the Mauch Chunk Group (Busanus 1974). The Bickett Shale is lithologically the most variable unit within the Bluefield Formation, exhibiting rapid lateral changes in lithology. This nonmarine unit consists primarily of red and green mudstones but medium-grained sandstones —which have been interpreted as fluvial point bar and overbank deposits--are also present (Busanus 1976). The tetrapod remains (which include fragments of *Greererpeton* and *Proterogyrinus)* recovered by the Museum of Comparitive Zoology were apparently found about 1m below the main vertebrate bearing bed quarried by the Cleveland Museum (C. Scaff, MCZ, personal communication). It is not known whether the fragmentary tetrapod remains collected by the Cleveland Museum were removed from the main layer or from the 'bone bed' below it.



Fig. 1. Quarrying operations by members of the Cleveland Museum of Natural History field party in a section of the Greer Limestone Company quarry, Monogalia County, West Virginia. Fossiliferous rock within the Bickett Shale is being removed from the West wall of the quarry. Circa 1970.

Because Viséan and Namurian tetrapods are exceedingly rare, a description of this material is important for it substantiates a more diverse assemblage than previously recognized at Greer. Recent descriptions of Scottish Carboniferous tetrapods by Panchen (1985) and Smithson (1985a, 1985b) permit a more precise taxonomic assignment for some of the tetrapod remains from Greer. Comparing taxonomic diversity indicates that Euramerican Lower Carboniferous and basal Upper Carboniferous tetrapod assemblages are similar.

I have opted to refrain from erecting formal taxonomic names because to do so on such fragmentary material would be premature. Although it seems unlikely, the isolated remains could represent elements from five different species.

## Description

### Vertebrae

CMNH 11239 (Figs. 2-5) consists of two large rhachitomous vertebrae. Both vertebrae conform to the typical rhaehitomous pattern, being composed of a relatively massive intercentrum and paired pleurocentra that bear large facets to support the neural arch. These vertebrae are clearly distinct from the essentially embolomerous vertebrae of *Proterogyrinus,* and their size and proportions preclude the possibility that they pertain to *Greererpeton.*

The three intercentra preserved in CMNH 11239 are massive and remarkably similar to those of *Eryops* (Moulton 1974) (Fig. 2, A-D). Ventromedially, a flat longitudinal ridge is only weakly developed and may represent the zone of fusion between paired anlagen. In lateral view, the ventral margin of the intercentrum is gently concave. The median ridge is flanked by two shallow concavities formed by periosteal bone that is deflected along the anterior and posterior margins of the intercentrum (Fig. 2, A and D). The periosteal bone is perforated by minute pits.

The concave ventrolateral surfaces vanish dorsally as the periosteal bone gathers to form a small semicircular facet that articulates with the capitulum of the rib (Fig. 2A). The parapophyses project little beyond the margin of the bone but can be seen in anterior or posterior view. A narrow strip of finished bone curves around each parapophysis to terminate on the apex of the wedge. On the two anterior-most intercentra, the facet for the capitulum of the rib is very small and only weakly developed (Fig. 2D).

The anterior, posterior, and dorsal (notochordal) surfaces are rough and unfinished. Because the intercentrum is very thick mediolaterally, the notochordal notch is relatively small. In typieal rhachitomous fashion, the massive intercentra from adjacent segments abut ventromedially (Fig. 5 A).
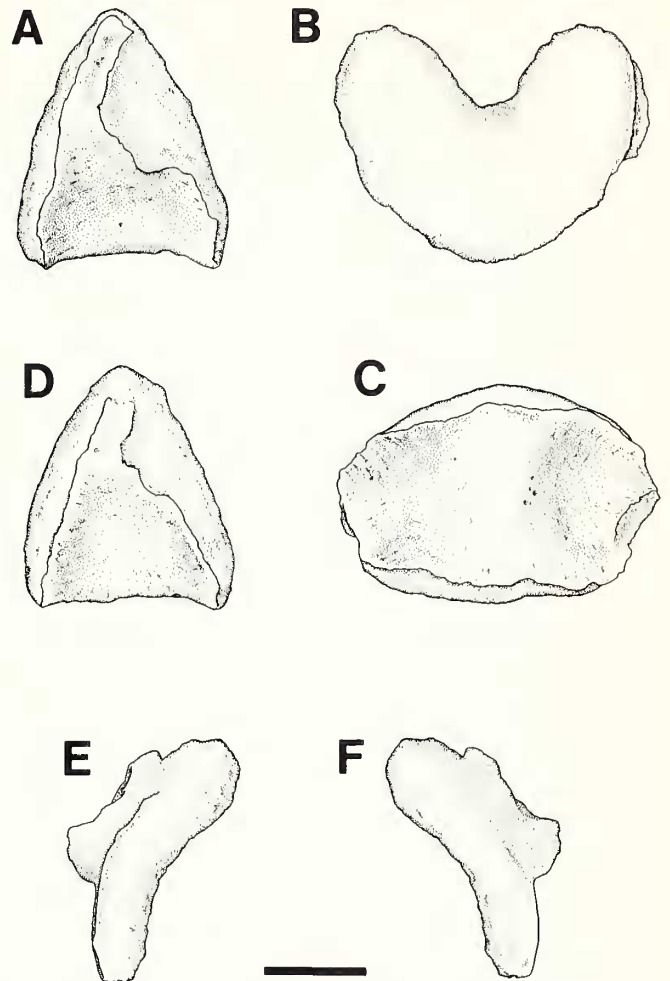


Fig. 2. CMNH 11239, elements of the centrum. A-C, a thoracic intercentrum in left lateral, anterior, and ventral views respectively; D, a cervical intercentrum in left lateral view; E-F, a pleurocentrum half in posterior and anterior views respectively. Scale bar equals 1 cm.

In life, the pleurocentra of CMNH 11239 were situated above the notochord and the main ossified portion of the intercentrum (Figs. 2 E-F and 5 A-B). In lateral view, each pleurocentrum half is an elongated oval that bears a protuberant semicircular articular facet on its anterodorsal margin that received the pedicle of the neural arch. This facet of unfinished bone forms an angle of approximately 60° with a plane tangential to the dorsolateral curvature of the external surface of the pleurocentrum. The external surface below and around the posterior margin of the facet is finished with smooth bone. Ventrally, the pleurocentrum ends in a blunt point. In anterior or posterior view the pleurocentrum is gently curved to surround the notochordal space. The internal surface is unfinished. Opposing antimeres of one pleurocentrum probably abutted above the notochord and immediately below the spinal cord (Fig. 5 B).
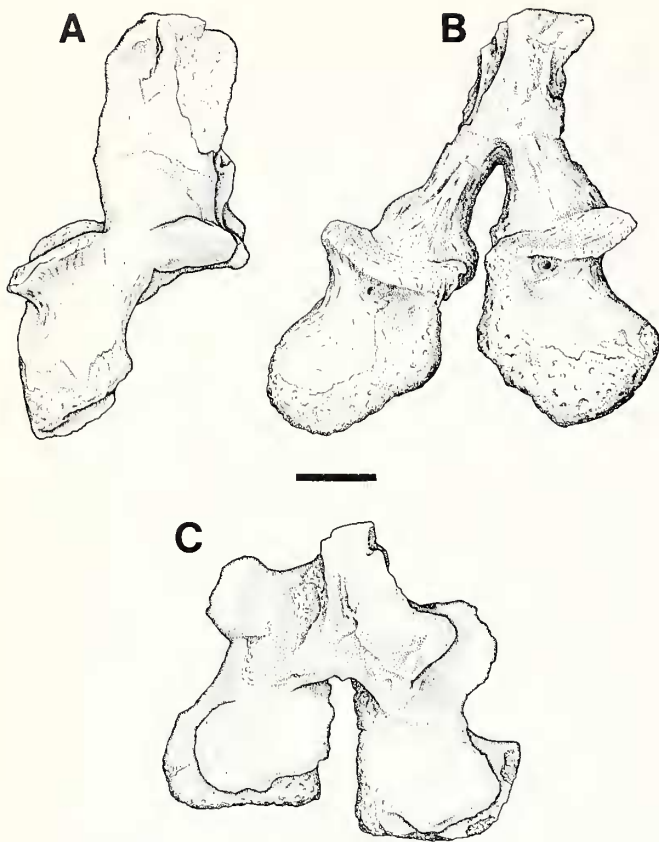
Fig. 3. CMNH 11239, A-C, specimen drawings of a 'thoracic' neural arch in left lateral, anterior, and dorsal views respectively. Scale bar equals 1 cm.

The two neural arches preserved in CMNH 11239 differ in the structure of the neural spine and pedicle (Figs. 3 and 4). The distal end of one of the neural spines is greatly expanded laterally and markedly rugose (Fig. 4), whereas the other is much more slender and laterally compressed (Fig. 3). Based on the structure of the neural arches in *Greererpeton* (Godfrey 1986), laterally expanded neural spines and poorly developed diapophyses occur in the cervical series, whereas narrow, laterally compressed spines and longer transverse processes characterize more posterior vertebrae. Because both spines are unfinished dorsally, each was probably capped by cartilage in life.

One of the more remarkable features of both arches is the retention of a large supraneural space (Figs. 3 B and 5 B). The space remains open for half the height of the spine as measured from the base of the postzygapophyses. A supraneural space (canal) is primitive for tetrapods and is thought to have accommodated a supraneural ligament (Smithson 1985a). In anterior view, the neural spine is roughly the shape of an inverted V. On the posteromedial surfaces of each spine, immediately above the postzygapophysis, is a conspicuous groove that passes dorsally to terminate where the arch halves meet above the supraneural space.

Both pre- and postzygapophyses are roughly ovoid in

outline and inclined very little from the horizontal. Immediately below each prezygapophysis is a deep pit which may have led to a foramen (Fig. 3 B). This feature is not known in any other early tetrapod.

Both arches possess large, broadly oval to rectangular facets on their ventromedial surfaces to receive the articular facets of the pleurocentrum. Immediately above the lateral margin of the pedicle is a narrow strip of periosteal bone. Above this strip the transverse process is poorly developed. In the cervical neural arch, the diapophyses are almost non-existent and probably did not hold the tuberculum of a rib in life (Fig. 4 A and B). On the other neural arch, protuberant flange-like diapophyses are developed. Judging from the relatively small size of these narrow, anteroventrally directed facets, the tuberculum must have been small.
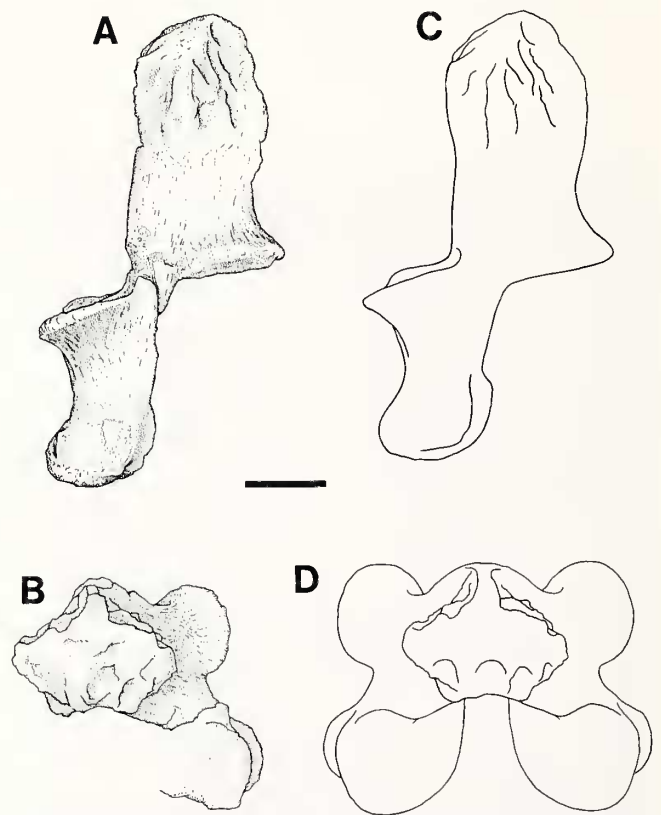


Fig. 4. CMNH 11239, A and C, specimen drawings of a cervical neural arch in left lateral and dorsal views respectively; B and D, restorations of the arch in lateral and dorsal views respectively. Scale bar equals 1 cm.

To summarize: although the vertebrae of CMNH 11239 resemble superficially those of *Eryops*, they differ from that genus in the possession of the following features: 1) a large supraneural space; 2) a relatively short neural spine; 3) widely separated contralateral pre- and postzygapophyses; and 4) a deep pit or foramen below each prezygapophysis. These vertebrae are probably derived from a large rhachitomous temnospondyl amphibian.
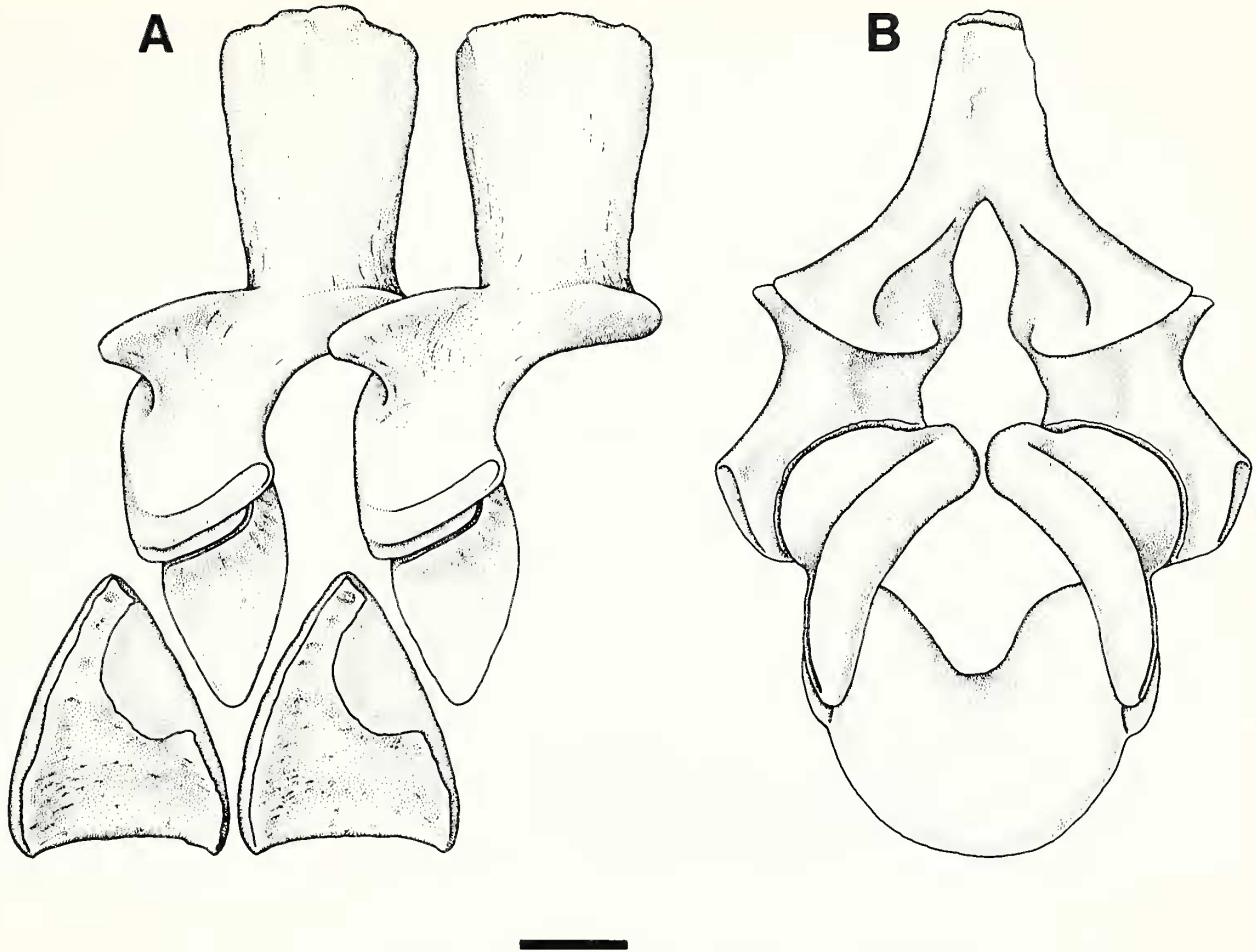
Fig. 5.   Restoration of vertebrae based on CMNH 11239; A, left lateral view; and B, posterior view. Scale bar equals 1 cm.

## Ribs

CMNH 11230 consists of a consecutive series of 10 or 11 large but incompletely preserved ribs lying on the visceral surface of an articulated series of ventral scales (Fig. 6). Although no rib heads are preserved, the morphology of the gastralia indicates that the right side of the body is represented and that the narrow end of the slab in Figure 6 is the anterior end. The ribs lack characteristic features of cervical, sacral, or caudal series and thus probably represent a segment from the midtrunk region. Although all the ribs are broken or variably crushed, they retain much of their original curvature. Because the radius of curvature of the eighth rib is just over 7 cm, the trunk diameter at that point was probably 15 cm or more if rib curvature followed that of the body. All the ribs are ornamented with longitudinal striations as in *Crassigyrinus* (Panchen 1985). The rib shafts lack an uncinate process or flange found in some temnospondyls. The large size of the ribs and the morphology of the gastralia indicates that they do not pertain to *Proterogyrinus.*

Although some of the scales are scattered, articulated series show that the original pattern was *en chevron* (Fig. 7 A). The scales are shaped much like an elongate tear drop. The anterolateral margin of each scale is more conspicuously convex than the trailing posteromedial edge. Their ventral surface is smooth and convex whereas their visceral surface is concave. A rounded ridge (Fig. 7 B) runs the length of the scale along the posterodorsal (internal) surface. In ventral view, the medial margin of each scale underlaps the trailing edge of its medial neighbor. The scales in CMNH 11230 resemble those of *Crassigyrinus.* Pending further discoveries, CMNH 11230 is tentatively assigned to the genus *Crassigyrinus.*

## Scapulocoracoid

MCZ 8950 (Fig. 8) is a single incompletely preserved right scapulocoracoid. The thin coracoid plate appears to be virtually complete, whereas the margin of the scapular blade anterodorsal to the supraglenoid buttress is poorly represented. The position of foramina and its overall proportions preclude it from belonging to either *Greererpeton* or *Proterogyrinus* (Fig. 8, D–F).

The glenoid is fairly well developed and forms a concave horizontal strap of unfinished bone that shows very little
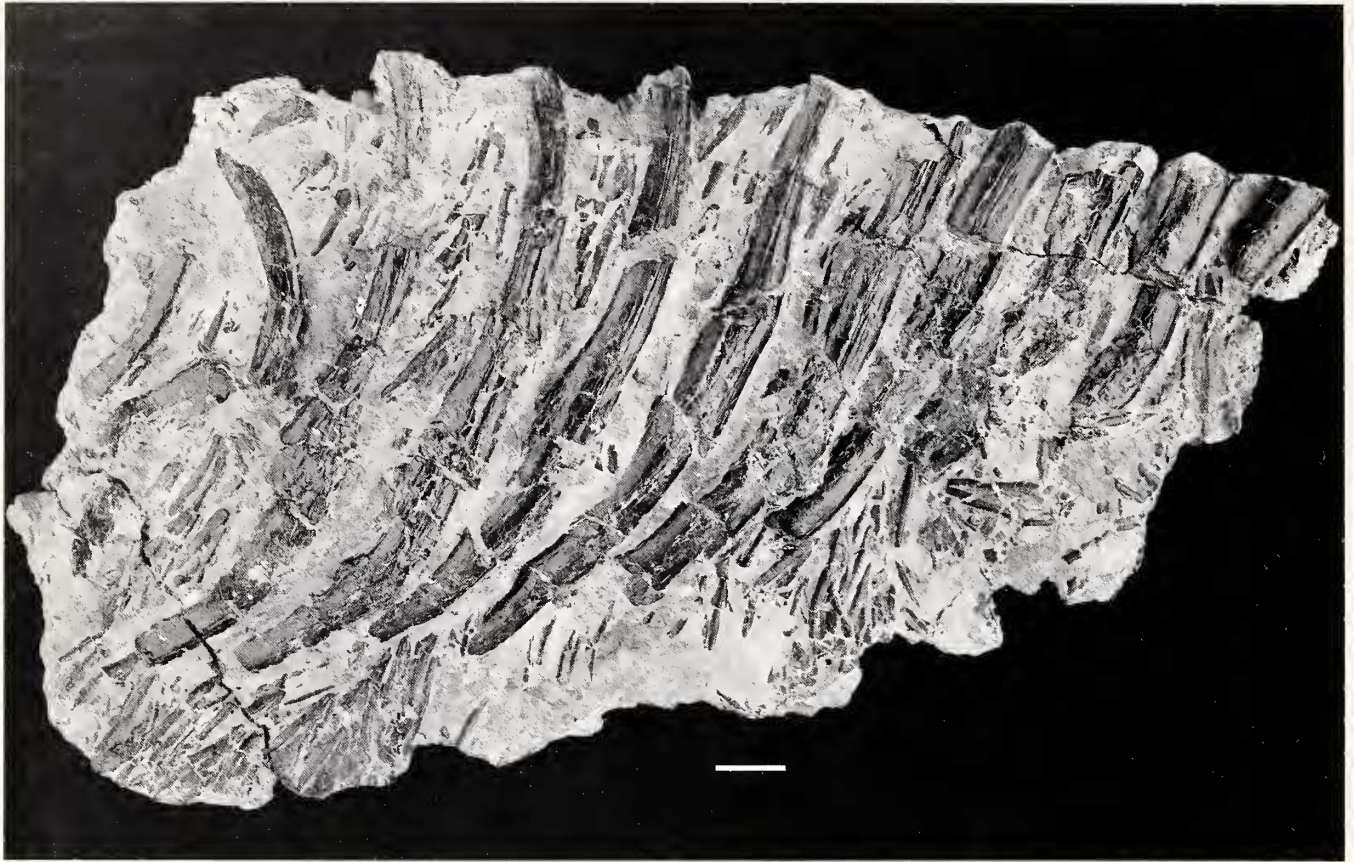
Fig. 6. CMNH 11230, 10 or 11 incomplete ribs and ventral scales from the right side of the body in dorsal view. Two ribs, 8 and 9 in the series (counting from the narrow end of the slab), were fractured in life and show a swollen mass of ankylosed bone distally. Scale bar equals 1 cm.

torque along its surface. Except for the anterior one-third of the glenoid, which is directed postero-ventrolaterally, the fossa is directed laterally.

Above the anterodorsal margin of the glenoid on the posterodorsal-facing margin of the ascending scapular blade, a small boss is developed that is visible in lateral view (Fig. 8 A and B). Extending posteriorly from the base of this small tuberosity, along the surface immediately medial to the glenoid, is a small ridge which ends on the posterior margin of the bone. A second, more prominent ridge lies medial and parallel to this ridge and continues from the posterior margin of the bone anterodorsally onto the supraglenoid buttress, where it loses prominence.

In medial view, the supraglenoid buttress thins rapidly anterior to the infraglenoid buttress. The ascending scapular moiety is not preserved. The supraglenoid buttress is not perforated by the supraglenoid foramen, but a C-shaped notch (Fig. 8 A), immediately anterior to the supraglenoid buttress and level with the glenoid articulation, may represent the remnants of this foramen. The foramen passes through the 3 mm thick bone in a ventrolateral direction. Alternatively, this foramen might represent the supracoracoid foramen, and the supraglenoid foramen may have been lost. A second large foramen is visible laterally, just
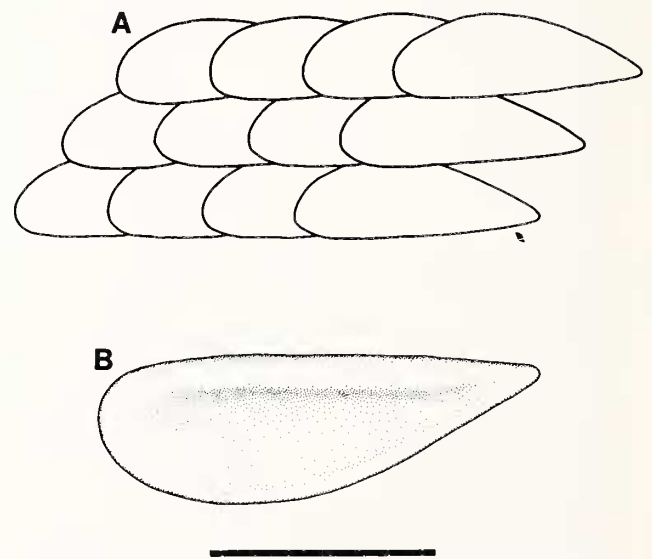


Fig. 7. Restoration of gastralia in ventral view based on CMNH 11230 (the narrow end of each scale points medially and the anterior end of the body lies towards the top right-hand corner of the page); and B, one scale enlarged, in dorsal view. Scale bar equals 1 cm.

beneath the anterior margin of the glenoid. It passes through the scapulocoracoid in a dorsomedial direction to open on the medial surface at the base of the supraglenoid buttress. The homology of this foramen is difficult to determine but, as in *Eoherpeton* (Smithson 1985a), it could represent the common opening of the supracoracoid and glenoid foramen.

The unfinished bone forming the thin ventromedial margin of the coracoid plate was probably finished by cartilage in life. Both medial and lateral surfaces of the plate are perforated by numerous 'nutritive' foramina. The antero-ventromedial portion of the scapulocoracoid is perforated by another fairly large foramen which passes vertically through the bone. Its location is almost identical to the anterior coracoid foramen seen in *Protorothyris archeri* (Clark and Carroll 1973, Figs. 5 A and 6 F).

## Humeri

MCZ 8951 (Fig. 9) is an incomplete right humerus that possesses several features that are not present in *Greererpeton* or *Proterogyrinus*.

On the dorsal surface of the humerus immediately above the proximal articulation is a conspicuous boss or tubercle. Immediately behind the tubercle is a concavity which may have marked the insertion of m. subcoracoscapularis. The processus latissimus dorsi is damaged in MCZ 8951. The ectepicondyle ridge begins at the base of the processus latissimus dorsi and broadens as it curves gently towards the anterodistal corner of the bone. Distally, the dorsal margin of the condyle was damaged and, therefore, the exact height of the ridge is not known.

A small posteriorly directed flange of bone is present on the postaxial surface of the humerus (Fig. 9 A and C). Aside from *Eoherpeton* (Smithson 1985a), this flange has not been described on the humerus of other early tetrapods; consequently, its function remains unclear. Between the aforementioned flange and the processus latissimus dorsi is a shallow longitudinal trough which deepens distally and marks the postaxial base of the ectepicondyle.

The deltopectoral crest in MCZ 8951 is remarkably large. Anteroventrally, the crest exhibits a shallow pit, above which lies a large tubercle. The pit and tubercle mark the major insertion of m. pectoralis and m. deltoideus respectively. A postaxially directed ridge extends from the deltoid tubercle across the dorsal surface of the humerus to merge with the anterior end of the ectepicondyle ridge at the base of the processus latissimus dorsi (Fig. 9 A). As in some early amniotes (Romer 1956), this ridge presumably marks the insertion of m. scapulohumeralis anterior.

The proximoventral surface of MCZ 8951 displays two prominent areas of muscle attachment. A pronounced preaxial tubercle marks the insertion of m. supracoracoideus and, more posteriorly, a broad concavity marks the insertion of m. coracobrachialis. The area of insertion of these and other muscles on MCZ 8951 is based on the description of other more completely known tetrapods
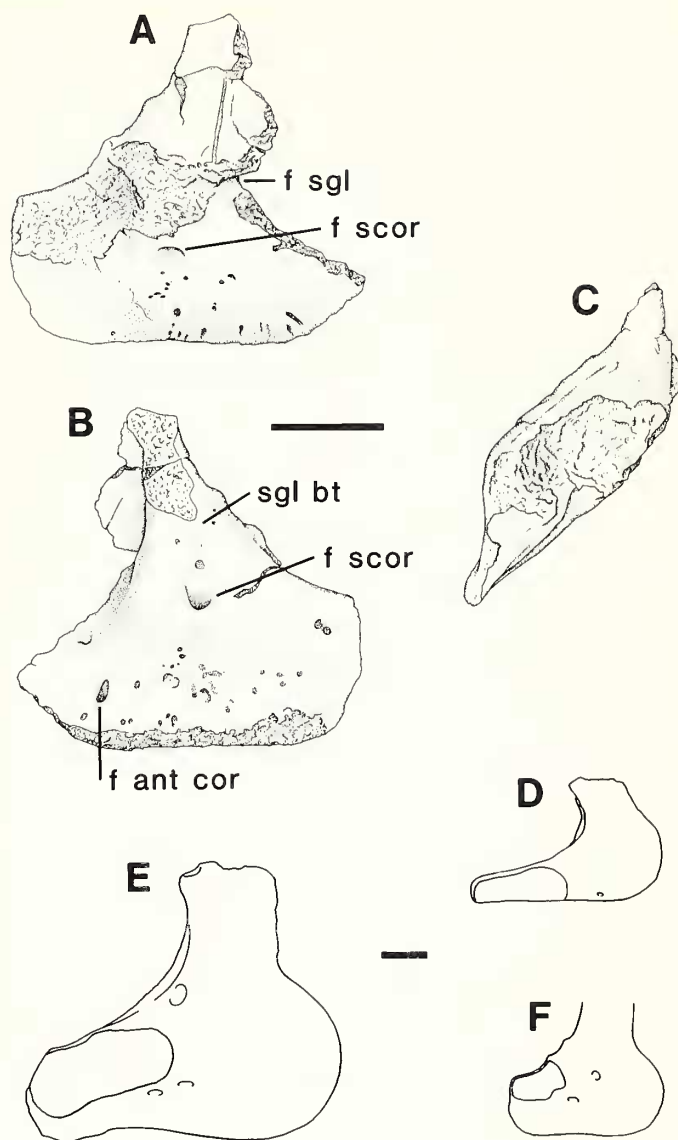


Fig. 8. MCZ 8950, A-C, specimen drawings of an incomplete right scapulocoracoid in lateral, medial, and posterior views respectively. Partially restored right scapulocoracoid of D, *Greererpeton burkemorani;* E, *Proterogyrinus scheelei;* and F, MCZ 8950, all drawn to the same scale. *P. scheelei* after Holmes (1980). Scale bars equal 1 cm. Abbreviations: anterior coracoid foramen, f ant cor; supracoracoid foramen, f scor; supraglenoid buttress, sgl bt; supraglenoid foramen, f sgl.

(Romer 1956; Holmes 1980; Smithson 1985a).

The supinator flange and entepicondyle are incomplete in MCZ 8951. The preserved section of the entepicondyle differs from that seen in *Eoherpeton* in that it extends distally as a smooth, broadly rounded flange beyond the trochlea (ulnar articulation), much as it does in *Eryops* (Miner 1925). The distal and postaxial margins of the entepicondyle are finished with periosteal bone that is rounded from dorsal to ventral surfaces. The entepicondyle foramen passes from the proximal anterodorsal surface of the entepicondyle in a ventrodistal direction. In ventral view, the foramen exits below a distinct ridge that sweeps
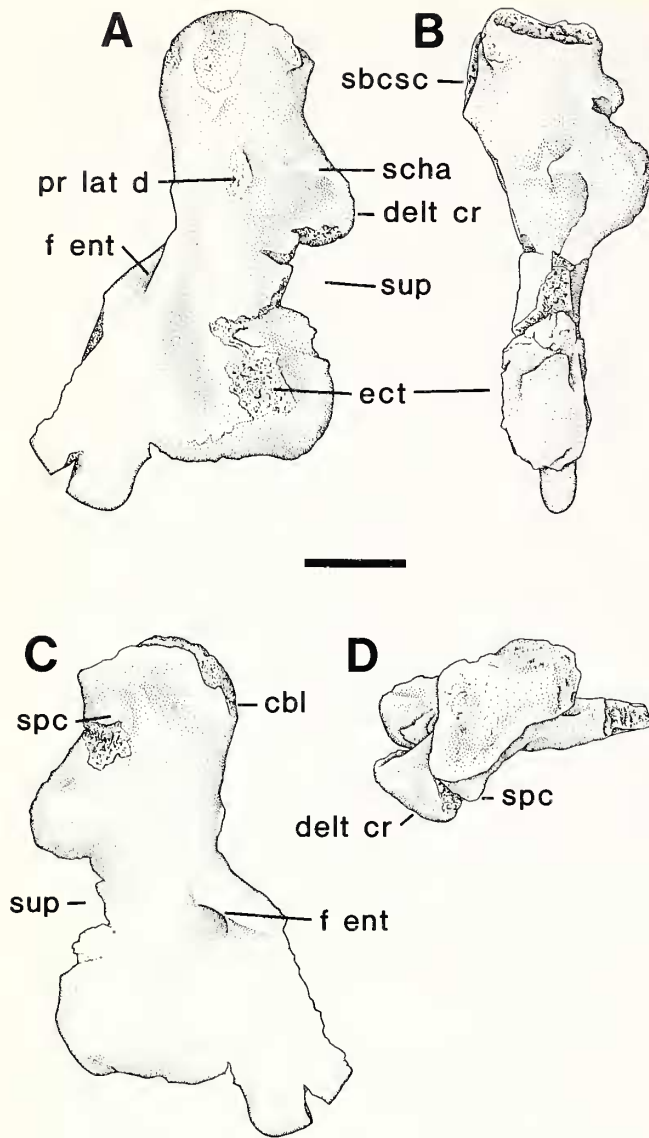
Fig. 9. MCZ 8951, A-D, specimen drawings of an incomplete right humerus in dorsal, preaxial, ventral, and proximal views respectively. Scale bar equals 1 cm. Abbreviations: deltopectoral crest, delt cr; ectepicondyle, ect; entepicondyle foramen, f ent; m. coracobrachialis, cbl; m. scapulohumeralis anterior, scha; m. subcoracoscapularis, sbcsc; m. supracoracoideus, spec; processus latissimus dorsi, pr lat d; supinator flange, sup.

be attributed to size. Among Lower Carboniferous tetrapods, only *Eoherpeton* approaches MCZ 8951 in the large number of conspicuous areas for muscle attachment. MCZ 8951 is provisionally assigned to this genus.
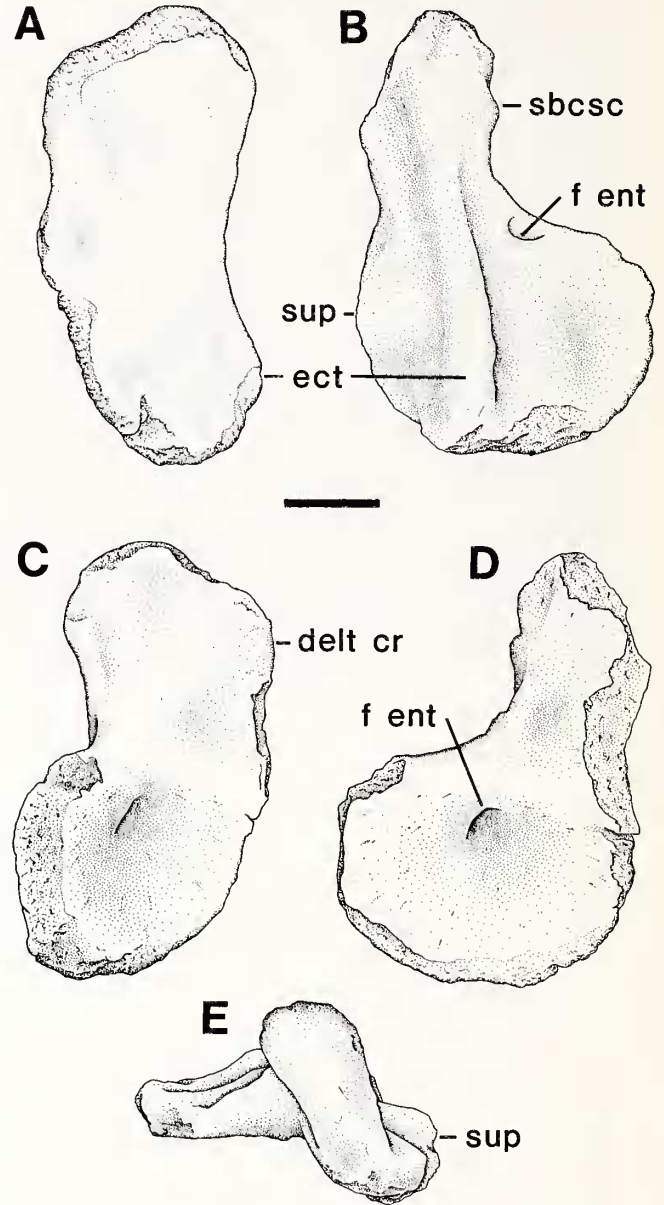


Fig. 10. MCZ 8952, A-E, specimen drawings of a left humerus in preaxial, dorsal, slightly ventral of the postaxial surface, ventral, and proximal views respectively. Scale bar equals 1 cm. Abbreviations as in Fig. 9.

postaxially along the proximal margin of the entepicondyle. As the entepicondyle is incomplete, the extent of this ridge is unknown. A shallow groove extends in an anterodistal direction across the ventral surface of the entepicondyle from the entepicondyle foramen to vanish below the ulnar articulation (Fig. 9 C). Radial and ulnar condyles are poorly defined. In MCZ 8951, the long axis of the proximal articulation forms an angle of 45-50° with the plane of the entepicondyle (Fig. 9 D).

Although somewhat smaller, MCZ 8951 bears a striking similarity to the humerus of *Eoherpeton* as described by Smithson (1985a). Minor differences between the two may

Although the second undescribed humerus from Greer (MCZ 8952, Fig. 10) is of the tetrahedral type common to most early tetrapods, it is unlike other humeri from this locality in that it is a more robust element with a higher degree of torsion and is without most of the tuberosities or ridges marking the origin or insertion of limb musculature.

If the plane of the entepicondyle is positioned horizontally, the unfinished convex strap of bone forming the proximal articulation is nearly vertical and remarkably compressed anteroposteriorly (Fig. 10 E). The articular surface is poorly defined. A short distance behind the postaxial margin of the proximal articulation is a small tuberosity, probably marking the insertion of m. subcoracoseapularis. This tuberosity forms a ridge that continues posterodistally to form the anterodorsal margin of the entepicondyle. On the preaxial side of this tuberosity, a shallow groove passes distally and becomes progressively more pronounced as it undercuts the ridge that forms the ectepicondyle. The posterodorsally projecting ectepicondyle is unfinished.

The deltopectoral crest in MCZ 8952 is poorly developed, and the insertions of m. pectoralis and m. deltoideus are not defined. A small ridge passes postaxially from the posteroventral corner of the deltopectoral crest onto the entepicondyle above the entepicondyle foramen. Anterior to this ridge the proximoventral surface of the bone in MCZ 8952 shows two V-shaped coneavities that are separated by a second low, rounded ridge. The anterior-most concavity is larger and lies immediately postaxial to the deltopectoral crest. The second concavity, with the top of its V-shaped margin directed proximally, lies adjacent to the small tuberosity that may represent the insertion of m. subcoracoseapularis. The deltopectoral crest and the supinator proeess are continuous, forming a large preaxial flange. The dorsal preaxial surface of the supinator flange bears a bulbous tubercle that may have held the origin of m. supinator.

The dorsal surface of the entepicondyle bears a broad but low ridge that extends proximodistally. This ridge increases substantially the thickness of the entepicondyle distally and presumably accommodated the radial, ulnar, or both radial and ulnar condyles.

MCZ 8952 displays a remarkably high degree of longitudinal torsion. The long axis of the proximal articulation forms an angle of about 64° with the plane of the entepicondyle.

## Discussion

The description of several additional tetrapods from Greer indicates that this assemblage is more diverse than previously recognized. In terms of its taxonomic complement, the Greer tetrapod fauna resembles two localities from the Midland Valley of Scotland and three North American localities (Table 1). The faunal similarities between Greer, Gilmerton (Smithson 1985b), Keokuk County (McKay et al. 1987), Cowdenbeath (Smithson 1985b, 1986), Point Edward (Carroll et al. 1972), and Hinton (Smithson 1982 and personal communication) are not all that surprising. All Viséan and Namurian tetrapods are derived from a narrow equatorial strip along the southern region of 'pre-drift' Euramerica (Milner et al. 1986). These sites extend from present-day Iowa in the west to the Federal Republic of Germany in the east and demonstrate that known localities are remarkably restricted latitudinally. Their faunas were dominated by large, primarily aquatic tetrapods.

TABLE 1
Distribution of Euramerican
Amphibians across the Viséan-Namurian Boundary

| STAGE | LOCALITY | TAXA | Crassigyrinus | Loxomma | Spathicephalus | Eoherpeton | Doragnathus | Proterogyrinus | Pholiderpeton | Undescribed Anthracosaur | Pholidogaster | Greererpeton | Large Temnospondyl | Adelogyrinidae |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Namurian | Hinton, West Virginia | | *? | | | *? | *? | *? | | | | * | | |
| | Point Edward, Nova Scotia | | | | * | | | | | * | | *? | | |
| | Cowdenbeath, Fife Region | | * | | * | * | * | * | | | | | | * |
| Viséan | Greer, West Virginia | | *? | | | *? | | | * | | | * | * | |
| | Keokuk County, Iowa | | | | | | | | | * | | *? | | |
| | Gilmerton, Lothian Region | | * | * | | * | | | | | * | | | |

## Acknowledgments

The ventral surface of the entepicondyle is conspicuously concave, with its deepest point marked by the opening of the entepicondyle foramen. The foramen passes from the ventral suface in a posterodorsal and slightly medial direction and opens near the proximal margin of the entepicondyle.

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